

1 **Title:** Skin wettedness is an important contributor to thermal behavior during exercise and recovery

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20 **Abstract:**

21 We tested the hypothesis that mean skin wettedness contributes to thermal behavior to a greater extent
22 than core and mean skin temperatures. In a $27.0\pm 1.0^{\circ}\text{C}$ environment, 16 young participants (8 females)
23 cycled for 30 min at $281\pm 51\text{ W}\cdot\text{m}^{-2}$, followed by 120 min seated recovery. Mean skin and core
24 temperatures and mean skin wettedness were recorded continuously. Participants maintained a thermally
25 comfortable neck temperature throughout the protocol using a custom made device. Neck device
26 temperature provided an index of thermal behavior. Linear regression was performed using individual
27 minute data with mean skin wettedness, core and mean skin temperatures as independent variables and
28 neck device temperature as the dependent variable. Standardized beta coefficients were used to determine
29 relative contributions to thermal behavior. Mean skin temperature differed from pre-exercise
30 ($32.6\pm 0.5^{\circ}\text{C}$) 10 min into exercise ($32.3\pm 0.6^{\circ}\text{C}$, $P<0.01$). Core temperature increased from $37.1\pm 0.3^{\circ}\text{C}$
31 pre-exercise to $37.7\pm 0.4^{\circ}\text{C}$ by end-exercise ($P<0.01$), and remained elevated through 30 min recovery
32 ($37.2\pm 0.3^{\circ}\text{C}$, $P<0.01$). Mean skin wettedness increased from pre-exercise ($0.14\pm 0.03\text{ a.u.}$) at 20 min into
33 exercise ($0.43\pm 0.09\text{ a.u.}$, $P<0.01$) and remained elevated through 80 min recovery ($0.18\pm 0.06\text{ a.u.}$,
34 $P\leq 0.05$). Neck device temperature decreased from $26.4\pm 1.6^{\circ}\text{C}$ pre-exercise to $18.5\pm 8.7^{\circ}\text{C}$ 10 min into
35 exercise ($P=0.03$) and remained depressed through 20 min recovery ($14.4\pm 11.2^{\circ}\text{C}$, $P<0.01$). Mean skin
36 wettedness ($52\pm 24\%$) provided a greater contribution to thermal behavior compared to core ($22\pm 22\%$,
37 $P=0.06$) and mean skin ($26\pm 16\%$, $P=0.04$) temperatures. Skin wettedness is an important contributing
38 factor to thermal behavior during exercise and recovery.

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40

41 **Keywords:** Thermoafferent feedback, thermoregulation, thermoregulatory behavior, exercise, recovery

42 **Introduction**

43 Skin wettedness is a measure of the proportion of the skin that is wet at any given time (16). In
44 most situations, skin wettedness occurs secondary to sweating and sweat buildup in the microclimate
45 (16). Gagge *et al.* (15) were the first to identify that increases in skin wettedness contribute directly to
46 increases in perceptions of thermal discomfort, independent of changes in body temperature. This was
47 later confirmed by Fukazawa and Havenith (12), who demonstrated a linear relationship between skin
48 wettedness and thermal discomfort. Despite this, the afferent stimulus for thermal discomfort is
49 commonly reported as the change in mean body temperature, a factor derived from the weighted average
50 of core and mean skin temperatures (2, 11, 18). This approach disregards the contribution of skin
51 wettedness to thermal discomfort. Further to this, studies aiming to model thermal comfort and physical
52 activity neglect the contribution of skin wettedness to thermal comfort, likely due to a lack of empirical
53 evidence (22, 34).

54 Thermal discomfort is the precursor to thermoregulatory behavior (30). In addition to autonomic
55 thermoeffectors (e.g. sweating, skin blood flow), thermal behavior aids in restoring and maintaining
56 thermal comfort during rest and exercise (10, 29). We previously showed that mean skin and core
57 temperatures contribute 30 and 70%, respectively, to thermal behavior during exercise and recovery
58 (35). However, we were unable to identify the contribution of skin wettedness in this study. Nevertheless,
59 skin wettedness has been proposed to be a significant factor in driving thermal behavior during exercise
60 (10, 14, 19). Skin wettedness cools the skin via evaporative mechanisms and the conscious awareness of
61 wettedness may outweigh the perceptual signals originating from changes in mean skin and/or core
62 temperature (15). The importance of skin wettedness to thermal behavior, relative to core and mean skin
63 temperatures, however, remains unknown. Therefore, the purpose of this study was to determine the
64 relative contributions of skin wettedness, core temperature, and mean skin temperature to thermal
65 behavior during exercise and recovery. We hypothesized that mean skin wettedness contributes to
66 thermal behavior to a greater extent than core and mean skin temperatures during exercise and recovery.

67

68 **Methods**

69 *Participants*

70 Sixteen young, healthy adults (8 females) completed this study. The participant characteristics
71 are listed in Table 1. All participants were physically active, normotensive, non-smokers, not taking
72 medications, cognitively normal, and free from any known cardiovascular, metabolic, neurologic or
73 psychological diseases. Female participants were not pregnant, which was confirmed via a urine
74 pregnancy test, and self-reported to be normally menstruating. To control for menstrual cycle hormones,
75 all trials for females were performed during the first 10 days following self-identified menstruation or
76 during the placebo phase of their oral contraceptives (n=4), a period in which estrogen and progesterone
77 are at their lowest levels. Each subject was fully informed of the experimental procedures and possible
78 risks before giving informed written consent. The study was approved by the Institutional Review Board
79 at the University at Buffalo, and performed in accordance with the standards set by the latest revision of
80 the declaration of Helsinki. Participants visited the laboratory on two occasions. Visit one was a
81 screening and familiarization visit and visit two was the experimental trial.

82

83 *Instrumentation and measurements*

84 Height and weight was measured with a stadiometer and scale (Sartorius Corp. Bohemia, NY,
85 USA), and body surface area was calculated accordingly (1). Skinfold thickness was measured in
86 duplicate at the chest, axilla, triceps, subscapula, abdomen, suprailiac, and thigh (Harpenden, Baty
87 International, UK), and percent body fat was estimated from body density (31), which was calculated
88 from the sum of skinfolds measurements for males (20) and females (21). Aerobic fitness was
89 determined using a ramped protocol (detailed below). Cognitive ability was measured using the
90 Montreal Cognitive Assessment (25). Urine specific gravity was measured in duplicate using a

91 refractometer (Atago USA, Inc., Bellevue, WA, USA) to test that participants were euhydrated prior to
92 performing the trial.

93 A 3-lead ECG (DA100C, Biopac Systems, Inc. Goleta, CA, USA) was used for monitoring heart
94 rate. Blood pressure was measured using manual sphygmomanometry every 10 minutes throughout the
95 protocol. Skin blood flow was measured continually on the dorsal aspect of the left forearm via laser
96 Doppler flowmetry (Periflux System 5010, Perimed, Stockholm, Sweden).

97 Metabolic data were obtained via a mouth piece with a one-way non-rebreathing valve (Hans
98 Rudolph, Inc. Shawnee, KS, USA) at the end of 10 min pre-exercise timepoint, at 15 and 30 minutes
99 during exercise and every 30 minutes during post-exercise. Minute ventilation was calculated from
100 expired airflow measured via a heated pneumotachometer (Hans Rudolph, Inc. Shawnee, KS, USA),
101 which was continuously integrated over 1 min and corrected to standard temperature, pressure, dry
102 (STPD). The fractions of expired oxygen and carbon dioxide (VacuMed, Ventura, CA, USA) were
103 continuously measured from a 3 L mixing chamber. Oxygen uptake and carbon dioxide production were
104 calculated using the Haldane Transformation. The rate of metabolic heat production was calculated from
105 oxygen uptake and the respiratory exchange ratio (RER) using a standard equation (7).

106 Approximately 60 min prior to any experimental testing, participants swallowed a telemetry pill
107 (HQ Inc., Palmetto, FL, USA) for the measurement of core temperature. Participants were restricted
108 from ingesting any fluids or food immediately after ingesting the pill and until the end of the protocol. In
109 the event that a subject had contraindications to swallowing a core temp pill, a rectal thermistor (Mon-a-
110 therm; Mallinckrodt Medical, Inc., St Louis, MO, USA) was inserted by the subject, 10 cm beyond the
111 anal sphincter (n=1). Mean skin temperature was measured as the equally weighted average of ten
112 thermochron iButtons (Maxim Integrated Products Inc., San Jose, CA, USA) attached to the left side of
113 the body on the lower shin, posterior calf, posterior thigh, anterior thigh, abdomen, chest, scapula, hand,
114 triceps and forehead (33).

115 Local sweat rate was measured by tightly securing a capsule that covered 3.9cm^2 of the skin on
116 the axilla and posterior shoulder on the left side of the body. Dry nitrogen was perfused through the
117 capsule at a rate of $0.5\text{L}/\text{min}$, allowing for measurement of the water vapour exiting the gas capsules to
118 be continuously measured by capacitance hygrometry (HMT130, Vaisala, Woburn, WA, USA). Local
119 sweat rate was calculated by multiplying the humidity output by the flow rate of the dry nitrogen and
120 dividing that value by the surface area of the capsule. The local sweat rates are reported as an average of
121 both areas.

122 Relative humidity of the skin was measured using 8 hydrochron iButtons (Maxim Integrated
123 Products Inc., San Jose, CA, USA) placed directly adjacent (within 1-2 cm) to the thermocron iButtons
124 used to measure skin temperature at the forehead, chest, upper arm, forearm, sub-scapula, abdomen,
125 anterior thigh and calf. At each location, the iButton was raised ~ 6 mm off the skin using a custom made
126 capsule that allowed airflow to pass through. The distance of 6 mm, as opposed to the standard 2 mm,
127 was chosen because it ensured that the humidity sensor of the iButton would not become artificially
128 supersaturated due to a droplet of sweat entering the hygrosensor. 6 mm was deemed acceptable based
129 on pilot testing performed in our laboratory that identified no differences between 2 mm and 6 mm in
130 the measured relative humidity. Relative humidity from the iButtons placed on each site were used to
131 determine the water vapour pressure of the skin using standard calculations as previously reported by
132 Filingeri et al. (8). Finally, local skin wettedness was calculated according to the methods of Gagge (16).
133 Whole body mean skin wettedness was calculated as the equally weighted average of all 8 local skin
134 wettedness sites.

135 Neck skin temperature was measured using a single thermocouple taped to the dorsal aspect of
136 the neck. Thermal behavior was objectively measured using techniques modified from those of Cabanac
137 et al. (4, 5), which are currently in use in our laboratory (29, 35). In this model, participants were
138 instructed to control the temperature of the dorsal aspect of the neck so that it is thermally comfortable
139 throughout the experiment. The neck was chosen because it is the only skin area known to be equally

140 and highly sensitive to both cooling and heating (24). Thus, neck skin and neck device temperatures
141 provide objective and continuous measures of thermal behavior (4, 5). Neck temperature was controlled
142 using a dual tubing system that was in constant contact with the subject's neck (20 cm x 10 cm). This
143 tubing system contains two unique series of tubing. One series was continually perfused with a
144 thermoneutral (34°C) water. The other series was perfused by a cold fluid (-20°C), and the flow of this
145 fluid was directly controlled by the subject via a two-way ball valve. This permitted a range of neck skin
146 temperatures (~35 to ~20°C) that were rapidly achieved (within ~15 s) when the neck was perceived to
147 be thermally uncomfortable. The temperature of the effluent fluid immediately following contact with
148 the neck was measured using a single thermocouple embedded in the tubing of the neck device. This
149 neck device temperature provided a precise indication of when, and the extent by which, participants
150 behaviorally thermoregulated (35).

151 Perceptual measures for the whole-body and neck were made every 10 min to the nearest 0.5
152 units using the following standard visual analogue scales: thermal sensation (1=cold, 4=neutral, 7=hot
153 (15)); thermal comfort (1=comfortable, 4=very uncomfortable (14)); and skin wettedness (+3=very wet,
154 +2=wet, +1=slightly wet, 0=neutral, -1=slightly dry, -2=dry, -3=very dry (26)).

155

156 *Familiarization Protocol*

157 At least 24 hrs prior to experimental testing, participants reported to the laboratory to perform a
158 peak oxygen uptake (VO₂peak) test and were familiarized with how to use the neck device, and with the
159 perceptual questionnaires. The VO₂peak test was used to determine the relative cycling intensity that
160 would elicit a moderate (~55% VO₂peak) relative exercise intensity. Participants completed a 5 min
161 warm up on the cycle ergometer at a resistance of their choice, followed by two minutes of rest, after
162 which 2 min of baseline measures were collected. The first stage of the VO₂peak protocol began
163 immediately following baseline measures. Participants chose a cadence between 70-80 rpm. The actual
164 cadence was maintained throughout the duration of the test and during the subsequent experimental trial.

165 The first stage began at 0.5 kp for females and 1.0 kp for males, and increased by 0.25 kp every minute
166 thereafter until volitional exhaustion, defined as the inability to maintain their cadence within 10 rpm of
167 the required cadence. VO_2peak was identified as the highest oxygen consumption value (per minute)
168 measured during the test. Following the VO_2peak test, participants relaxed in a chair where the neck
169 device was placed on them and they were permitted to open and close the valve as they wished. At this
170 point in time, they were familiarized and asked to respond to each perceptual scale.

171

172 *Experimental protocol*

173 Participants arrived at the laboratory for their experimental trial euhydrated, confirmed via urine
174 specific gravity <1.020 (actual urine specific gravity: 1.011 ± 0.007), and having refrained from
175 strenuous exercise, alcohol and caffeine for 12 h, and food for 2 h. All experimental testing was
176 conducted during the winter months in Buffalo, NY (outside temperature on experimental days: $-2 \pm$
177 5°C). Participants wore a standard short sleeved crew t-shirt and running shorts (men or women's cut),
178 and their own socks and athletic shoes (~ 0.4 clo).

179 The experimental trial took place in a moderate thermal environment ($27.0 \pm 1.0^\circ\text{C}$, $22 \pm 4\%$
180 relative humidity). Following instrumentation, participants sat on a mesh chair behind a standard upright
181 cycle ergometer (Monark 828E, Sweden) for 10 min. Participants were then carefully transferred to the
182 cycle ergometer for 30 min of moderate intensity cycling at 81 ± 22 W ($55 \pm 7\%$ $\text{VO}_{2\text{max}}$, 281 ± 51
183 $\text{W}\cdot\text{m}^2$). This was followed by 120 min seated recovery on the aforementioned mesh chair. Participants
184 were allowed to watch non-stimulating documentaries throughout the entire protocol.

185

186 *Data and statistical analyses*

187 Continually recorded data were binned as 60 s averages every 10 min. These data are reported as
188 absolute values. The temporal data were analyzed for changes over time using one-way repeated

measures ANOVAs. For the temporal data, when a significant F test was identified, a priori Sidak post hoc comparisons were made between pre-exercise (i.e., 10 min pre-exercise) and end-exercise (i.e., 30 min exercise) time points. To determine the relative contributions of mean skin wettedness, core temperature and mean skin temperature to thermal behavior, continually recorded data were binned as 60 s averages every minute throughout. Multiple linear regression analyses were performed from these data for each individual participant, inclusive of all pre-exercise, exercise and recovery timepoints. The independent variables were mean skin wettedness, core temperature and mean skin temperature and neck device temperature was the dependent variable. All independent variables were log transformed to reduce confounding issues associated with multicollinearity in the dataset that could affect the resulting beta coefficients (32). The absolute value of each standardized beta coefficient for mean skin temperature, core temperature and mean skin wettedness from each individual multiple linear regression model were used to calculate the relative contribution of each independent variable for each subject. For example, the relative percent contribution of a given independent variable (e.g., 'a') was calculated from the standardized beta coefficient for this variable (e.g., β_a) as a function of the sum of all of the standardized beta coefficients (e.g., $\beta_a \div (\beta_a + \beta_b + \beta_c) \times 100$). This was completed for each variable and in each subject. The mean of all individual relative contributions were taken to provide an overall percent contribution of each variable to thermal behavior (i.e. neck device temperature). A similar analysis has been used previously to delineate the relative contributions of core and mean skin temperature on thermal comfort (11) and thermal behavior (35). Mean data for the individual standardized beta coefficients and the relative contributions were analyzed using a one-way repeated measures ANOVA. Pearson's correlation analyses were also run on individual data collected every 10 min during rest, exercise and recovery between the following variables: mean skin wettedness and perceived whole body skin wettedness, mean skin wettedness and perceived thermal comfort. For these analyses, perceptual values were changed to percentages for comparison with mean body wettedness and thermal behavior. Spearman's correlations for non-parametric data were run on perceived whole-body

214 skin wettedness and perceived thermal comfort data. Mean R^2 values and P-values were pooled to
215 determine the strength of the relationships. Multiple linear regression analyses were carried out using
216 SPSS (Version 22, IBM Analytics, Armonk, NY), while all other analyses were carried out using Prism
217 (Version 7, GraphPad Software Inc., La Jolla, CA). For all analyses, *a priori* statistical significance was
218 set at $P \leq 0.05$ and actual P-values are reported where possible.

219

220 **Results**

221 *Body temperatures and mean skin wettedness*

222 Mean skin temperature decreased from pre-exercise at 10 min during exercise ($P < 0.01$) and was
223 not different from pre-exercise during recovery at any time point ($P \geq 0.42$). Mean skin temperature also
224 did not differ from the end of exercise at any time during recovery ($P \geq 0.72$) (Figure 1A). In contrast,
225 core temperature was elevated over pre-exercise levels 10 min into exercise and remained elevated until
226 30 min post-exercise ($P \leq 0.04$). Core temperature decreased from end-exercise values within the first 10
227 min in the post-exercise period and continued to fall towards pre-exercise levels thereafter ($P < 0.01$)
228 (Figure 1B). Mean skin wettedness increased above pre-exercise levels 20 min into exercise and
229 remained elevated until 80 min into recovery ($P \leq 0.05$). Mean skin wettedness peaked at the end of
230 exercise and, compared to this point, was decreased at 20 min into recovery and thereafter ($P \leq 0.01$)
231 (Figure 1C).

232

233 *Thermoeffectors*

234 Neck device temperature was lower than at pre-exercise 10 min into exercise and remained
235 depressed until 20 min into recovery ($P \leq 0.03$). Following the cessation of exercise, neck device
236 temperature began to climb back toward pre-exercise levels but was only different from end-exercise
237 after 60 min into recovery ($P \leq 0.04$) (Figure 2A). Neck skin temperature was lower than at pre-exercise
238 20 min into exercise and remained lower until 30 min into recovery ($P \leq 0.03$). Compared to the end of

239 exercise, neck skin temperature was only different between 80 and 110 min into recovery ($P \leq 0.02$)
240 (Figure 2B). Average local sweat rate was elevated over pre-exercise levels at 10 min into exercise and
241 peaked at the end of exercise ($P < 0.01$), whereafter it decreased back towards pre-exercise levels within
242 the first 10 min of recovery and remained thereafter ($P \geq 0.35$) (Figure 2C). Forearm skin blood flow
243 increased and peaked at 30 min of exercise ($P < 0.01$) and remained elevated until 20 min into recovery
244 ($P \leq 0.04$) (Figure 2D).

245

246 *Thermal perceptions*

247 The neck was perceived to be thermally comfortable at baseline and did not change during
248 exercise ($P > 0.66$) or recovery ($P > 0.99$) (Figure 3A). Participants also perceived their whole body to be
249 thermally comfortable prior to exercise. However, whole-body thermal discomfort increased throughout
250 all of exercise ($P \leq 0.04$), and returned to pre-exercise levels with the first 10 min of recovery, where it
251 remained thereafter ($P \geq 0.93$) (Figure 3B). Thermal sensations of the neck were perceived to be neutral
252 at baseline and throughout exercise ($P > 0.99$) and recovery ($P > 0.99$) (Figure 3C). Whole body thermal
253 sensation was perceived to be neutral before exercise, and warmth sensations became evident at 20 min
254 of exercise ($P < 0.01$), peaking at end-exercise ($P = 0.03$). Perceptions of whole body thermal sensation
255 returned to pre-exercise levels at 10 min and remained throughout recovery ($P \geq 0.80$) (Figure 3D).
256 During pre-exercise, neck skin wettedness was perceived to be slightly dry, but became slightly wet 20
257 min into exercise and remained throughout the first 10 min into recovery ($P \leq 0.03$), but returned to
258 baseline afterwards ($P \geq 0.63$) (Figure 3E). Similar to perceptions of neck skin wettedness, perceptions of
259 whole body skin wettedness were perceived to be slightly dry prior to exercise and increased between
260 slightly wet and wet by the end of exercise ($P \leq 0.03$). Perceptions of whole body skin wettedness
261 decreased within 20 min and remained throughout recovery ($P \geq 0.44$). Compared to the end of exercise,
262 perceptions of whole body wettedness decreased within the first 10 min of recovery and remained
263 throughout ($P < 0.01$) (Figure 3F).

264

265 *Relative contributions to thermal behavior*

266 Core temperature data from 2 participants were only collected every 10 min. Therefore, these
267 data were excluded from the relative contributions analysis (n=14). The mean of all models for
268 combined individual data was significant ($R^2 = 0.636 \pm 0.194$, $P < 0.01 \pm 0.00$). The standardized beta
269 coefficient for mean skin wettedness (0.673 ± 0.349) was greater than both core (0.269 ± 0.271 , $P=0.04$)
270 and mean skin temperature (0.354 ± 0.257 , $P=0.03$), but did not differ between mean skin temperature
271 and core temperatures ($P=0.72$) (Table 2). Mean skin wettedness ($52 \pm 24\%$) contributed to thermal
272 behavior to a greater extent than mean skin temperature ($26 \pm 16\%$, $P=0.04$), but not core temperature
273 ($22 \pm 22\%$, $P=0.06$). The core and mean skin temperature contributions to thermal behavior did not
274 differ ($P=0.93$) (Figure 4).

275

276 *Correlations of skin wettedness, thermal behavior and perceptions*

277 One individual did not perceive thermal comfort to change during the protocol and was therefore
278 not included in the analysis (n=15). A moderate, positive correlation was found between the total
279 percentage of whole body skin wettedness and perceptions of whole body skin wettedness ($R^2=0.441 \pm$
280 0.240 ; $P=0.057 \pm 0.105$). Likewise, perceptions of whole body skin wettedness and whole body thermal
281 comfort were found to be moderately correlated ($R^2=0.461 \pm 0.249$ $P=0.069 \pm 0.134$). However, only a
282 weak relationship was found between the the total percentage of whole body skin wettedness and
283 perceptions of whole body thermal comfort ($R^2=0.284 \pm 0.166$; $P=0.12 \pm 0.21$).

284

285 **Discussion**

286 The present study aimed to determine the extent to which mean skin wettedness contributes to
287 thermal behavior during exercise and after exercise, compared to core and mean skin temperatures. In

support of our hypothesis, we have identified that mean skin wettedness contributes to thermal behavior to a greater extent compared to mean skin and core temperatures. These findings highlight the importance of measuring skin wettedness when examining mechanisms and contributing factors to thermal behavior, particularly during situations that elicit sweat production and accumulation (e.g., exercise, passive heat stress).

293

Importance of skin wettedness to thermal behavior during exercise and recovery

In the present study, participants cycled at a moderate exercise intensity that was sufficient to elevate core temperature and stimulate sudomotor activity. Participants were required to maintain the thermal comfort of their neck (i.e., a 1.0 on the thermal comfort scale), and were reminded to thermally behave by turning a neck cooling device on or off as necessary. Using this model, we have previously shown that core temperature contributed to thermal behavior to a greater extent than mean skin temperature during and following 60 min of low intensity exercise (35). This approach, however, omitted the potential contribution of skin wettedness to thermal behavior. In fact, skin wettedness has generally been overlooked as a contributor to thermal behavior despite its known contributions to thermal discomfort (12). This is likely due to our relatively little understanding of how skin wettedness afferent information is transmitted. Specifically, unlike thermoreceptors that send information directly back to the central nervous system to be integrated and bring about thermoeffector activation, humans do not possess hygroreceptors that provide wettedness afferent feedback (6). Rather, humans learn to perceive skin wettedness based on the integration of thermo- and mechano-receptor information (8). Nevertheless, it has been suggested that skin wettedness (and the perception thereof), occurring secondary to the buildup of sweat on the skin, plays a key role in thermal behavior alongside thermal afferent feedback during exercise, particularly in the heat (10). To our knowledge, this is the first study to directly examine the relationships between mean skin wettedness, core temperature, mean skin temperature, and thermal behavior. As such, the present data reveal that ~52% of the contribution to

313 thermal behavior, or the desire to receive cooling on the neck, was stimulated by mean skin wettedness,
314 with only ~26% and ~22% coming from mean skin and core temperatures, respectively. It is notable
315 that, although the comparison of relative contributions between mean skin wettedness and core
316 temperature only approached statistical significance ($P=0.06$), the standardized beta coefficients were
317 different between these variables ($P=0.04$). Collectively, therefore, we interpret these findings that mean
318 skin wettedness contributes to thermal behavior to a greater extent than both core and mean skin
319 temperatures.

320 It is thought that increases in skin wettedness during exercise cause thermal discomfort in spite
321 of reductions in skin temperature occurring secondary to sweat evaporation (16). A threshold skin
322 wettedness value of ~0.36 a.u. appears to elicit thermal discomfort during exercise at a rate of metabolic
323 heat production of ~175 W·m² (12). In support of this, metabolic heat production in the present study
324 was 281 ± 51 W·m² and mean skin wettedness peaked at 0.48 ± 0.08 a.u. (i.e., sweat covering ~48% of
325 the body surface) by the end of exercise. With these increases in metabolic heat production and whole
326 body skin wettedness, our observations of perceptions of 'slightly uncomfortable' for whole body
327 thermal discomfort during exercise are in line with other investigations (13, 17).

328 During recovery from exercise, thermal behavior is thought to promote the restoration of core
329 temperature and improve thermal comfort, which occurs at a time when autonomic heat loss
330 thermoeffectors are effectively 'switched off' (35). To our knowledge, the data presented in the current
331 study are the first to show that mean skin wettedness remains elevated well into the recovery period
332 (Figure 1). The difference between the temporal dynamics of average local sweat rate and mean skin
333 wettedness are perhaps most striking. Post-exercise, at a time when core temperature remains elevated
334 and sudomotor activity is withdrawn, the skin remains wet for some time thereafter. This suggests that
335 there may remain a medium to promote sweat evaporation, despite that sweat rate has returned to pre-
336 exercise levels. That said, some of this wettedness is likely the result of sweat buildup in the
337 microclimate, which ultimately may not provide the same rate of evaporative cooling as bare skin.

338 Nevertheless, mean skin wettedness appears to be important for the continued activation of thermal
339 behavior post-exercise, although the independent factor of bare vs. clothed skin warrants further
340 investigation. In summary, this is the first study to quantify the relative importance of mean skin
341 wettedness to thermal behavior during exercise and recovery. Our findings suggest that even at
342 moderate exercise intensities and in a moderate thermal environment, whole body skin wettedness is an
343 important factor in contributing to thermal behavior alongside changes in core temperature and mean
344 skin temperature.

345

346 *The importance of skin wettedness on perceptions of skin wettedness and thermal comfort*

347 Humans perceive skin wettedness through mechanoreceptor activation and reductions in skin
348 temperature (8, 9). Previous analyses have demonstrated strong positive correlations between increases
349 in whole body skin wettedness and thermal discomfort (12, 17). Further to this, it has been shown that
350 the pressure of clothing (i.e., tight versus loose fitting) can influence wetness perception (8). However,
351 specific fabric textiles (i.e., rough versus smooth) used in clothing do not significantly contribute to
352 wetness perception during dynamic activities, although they can increase sensations of pleasantness and
353 therefore, thermal comfort (27). Interestingly, our analyses did not reveal that skin wettedness and
354 thermal discomfort were strongly correlated in the present study ($R^2=0.284 \pm 0.166$, $P=0.12 \pm 0.22$).
355 One reason for this may be because we modeled our data individually in order to determine mean
356 correlations. Furthermore, we employed a relatively short exercise duration and only had modest
357 increases in thermal discomfort, despite similar levels of mean skin wettedness to the aforementioned
358 studies during exercise. Still, we were able to demonstrate a moderate positive correlation between
359 whole body skin wettedness and whole body wettedness perceptions ($R^2=0.441 \pm 0.240$, $P=0.057 \pm$
360 0.105), and between whole body wettedness perception and perceptions of thermal discomfort
361 ($R^2=0.461 \pm 0.249$, $P=0.069 \pm 0.134$). Collectively, these findings raise the question regarding whether
362 the perception of skin wettedness or actual skin wettedness is the more important mediator of thermal

discomfort and/or thermal behavior. In fact, it may be that actual skin wettedness is less important than the perceived magnitude of skin wettedness. For instance, considering that thermal behavior during exercise is driven by increases in thermal discomfort (30), it is likely that the perceived thermal discomfort is contributed to by perceptions of warmth and skin wettedness. Skin wettedness perception is brought about by acute reductions in skin temperature and/or mechanoreceptor stimulation, which normally occurs secondary to actual skin wettedness caused by sweat evaporation and buildup on the skin, respectively. Thus, any situation that results in reductions in skin temperature and/or mechanoreceptor stimulation could theoretically stimulate thermal behavior independent of actual skin wettedness. This remains to be elucidated. Clearly, therefore, the specific mechanisms and interactions between actual skin wettedness, perceived skin wettedness and thermal behavior deserve further investigation.

Considerations

In this study, mean skin wettedness was calculated as the mean of 8 sites collected using iButtons raised about 6mm off the skin. While we are confident that this represents actual wettedness, it is important to note that 5 of these sites were under clothing. Collecting data under clothing represents a real-life situation, and hence we deemed this appropriate. For instance, it is not uncommon for individuals to remain in their clothing after exercising, especially at moderate exercise intensities. However, there is a possibility that outside of the laboratory, individuals would change out of their clothing secondary to sweat buildup and/or sweat perception, which in itself may be evidence of the important contribution that mean skin wettedness imparts on thermal behavior. Additionally, it is important to draw attention to the fact that the findings presented herein are constrained to the conditions employed (i.e., moderate exercise intensity on a cycle ergometer, in a moderate thermal environment by young, healthy and active participants). Therefore, it is unknown if these weightings hold true during passive heat stress or exercise in the heat. Further research is warranted using different exercise

intensities, environments, or other situations in which heat stress results in changes in body temperatures and subsequent activation of sweating. A potential limitation of the present study is our use of a telemetry pill to measure core temperature. This is particularly important considering the relatively slower responsiveness to changes in body heat content of the telemetry pill compared to esophageal temperature (23). It is possible, therefore, that our measure of core temperature was underestimated during transitions from rest to exercise and overestimated during transitions from exercise to recovery. That said, because participants ingested the pill 60 min prior to the study, the limited transit time into the GI tract is believed to have better responsiveness time than rectal temperature (3) and supports our use of the pill therefore. Additionally, we only had female participants self-report menstrual cycle phase, and therefore do not know their hormone levels at the time of testing. It should also be noted that these findings are not causal. Rather, we have demonstrated that mean skin wettedness explains a greater proportion of the variability in thermal behavior when compared to mean skin and core temperatures. This was demonstrated using multiple linear regression analysis on time-series data sampled at a relatively high frequency. It is worth mentioning that using time-series data may have inflated the significance values reported herein. That said, the use of time-series data was deemed appropriate because collecting one data point per subject per time point was not feasible and because we modeled our data on a per subject basis (i.e., not pooled). Moreover, to reduce the potential confounding influence of multicollinearity on the beta coefficients arising from the linear regression models, we used data obtained throughout exercise and recovery, as opposed to analyzing the exercise and recovery time periods separately (32). This prevents conclusions regarding whether the contributions of skin wettedness, core temperature, and mean skin temperature differ between rest and recovery. Notably, however, such differences appear unlikely (35). It is clear, therefore, that despite the utility of using multiple linear regression in the present study, this approach is not without limitations. Thus, further studies are required to experimentally examine the contributions of skin wettedness, skin temperature, and core temperature by independently manipulating these variables and measuring the thermal

behavioral outcome. Finally, the variability in the beta coefficient of determination in linear regression analysis highlights the percentage that factors outside our present variables may contribute to thermal behavior. Our models revealed significant R^2 values for the model ($R^2 = 0.636 \pm 0.194$, $P < 0.01 \pm 0.00$). These values suggest that the combination of mean skin and core temperatures and mean skin wettedness contribute ~64% to thermal behavior during exercise and recovery. Hence, while these variables appear to account for a large quantity of the variation, there are likely other thermal or non-thermal factors that may also contribute to thermal behavior. This deserves further investigation.

Perspectives

To this point, the afferent stimulus for thermal behavior has been quantified only using mean body temperature, a weighted average of core and mean skin temperatures (35). Considering the findings from the present study, however, it is advisable that when examining the control of thermal behavior when body temperature increases and sweat production is expected, the thermal afferent stimulus should include a measure of mean skin wettedness. Although tightly constrained to the present exercise intensity, modality and environmental conditions, this study is the first to identify a new combination of thermal and skin wettedness stimuli that is likely to be more representative of the integrated afferent stimuli that contributes to thermal behavior. In conditions similar to those employed in the present study, it would be advisable that the mean afferent stimuli be used, rather than only the mean body temperature. This mean afferent stimulus should include mean skin temperature, core temperature, and mean skin wettedness weighted in the following manner: mean skin temperature: 0.26, core temperature: 0.22 and mean skin wettedness: 0.52. These weightings represent the average of the relative contribution to exercise and recovery as we were unable to tease out exercise compared to recovery to reduce the error associated with multicollinearity within our data sets. Despite this evidence, there remains a considerable amount of work to be done regarding the extent to which skin wettedness is a driver of thermal behavior. For instance, it is important to identify how these relative weightings may

differ in alternate modes and intensities of exercise, environmental conditions and with different types or levels of clothing coverage. The findings from the present study also highlight the need to further understand mechanisms underlying relationships between physiological changes (i.e., change in actual mean skin wettedness and actual mean body temperatures) and the perceptions that drive thermal discomfort and thermal behavior. A more thorough understanding of these mechanisms will provide the necessary tools to study how changes in these variables alter thermal behavioral responses and the motivation to behave in both healthy and ‘at risk’ populations (e.g., Multiple Sclerosis, cardiovascular disease, older adults, etc.).

Conclusions

This study demonstrates that mean skin wettedness likely contributes to thermal behavior to a greater extent than both mean skin temperature and core temperature during and after exercise that results in sweat production and accumulation on the skin and within the microclimate. Furthermore, this study provides further evidence that skin wettedness is associated with perceptions of skin wettedness and thermal discomfort. Considering the present findings, it is suggested that future research aiming to study the mechanisms and contributing factors to thermal behavior in humans should incorporate measures of skin wettedness, in addition to mean skin temperature and core temperature, particularly in instances when sweat production is expected.

Acknowledgements

The authors would like to thank all participants for their participation. We would also like to thank lululemon athletica inc. for their funding to support the study. Rob Gathercole is the Research Director for the Whitespace Innovation Team at lululemon athletica inc. Zachary Schlader, Rob Gathercole, Blair Johnson, and Nicole Vargas contributed to the conceptualization of this study. Chris Chapman and Nicole Vargas were responsible for data collection. Nicole Vargas performed data

463 analysis and drafting of the manuscript. All authors approved the final manuscript. Zachary Schlader has
464 received travel reimbursement from lululemon athletica inc. The results of this study are presented
465 clearly, honestly, and without fabrication, falsification, or inappropriate data manipulation.

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547

548

549 **Table 1** Subject characteristics, mean \pm SD. ^bAll participants were in the normal range for their age
550 ground (≥ 25 points) (28).

551

552 **Table 2** Standardized beta coefficients (absolute values) from individual linear regressions for relative
553 contributions of mean skin wettedness, core temperature and mean skin temperature to neck device
554 temperature (n=14). Mean skin wettedness, core temperature and mean skin temperature are independent
555 variables and neck device temperature is the dependent variable. *Different from core (P=0.04) and
556 mean skin temperatures (P=0.04).

557

558 **Figure 1** Mean skin temperature (A), core temperature (B), and mean skin wettedness (C) during
559 exercise and recovery (n=16, mean \pm SD). ^PDifferent from pre-exercise (P \leq 0.05). ^EDifferent from end-
560 exercise (P<0.01).

561

562 **Figure 2** Neck device temperature (A), neck skin temperature (B), average local sweat rate (C) and
563 forearm skin blood flow (D) during exercise and recovery (n=16, mean \pm SD). ^PDifferent from pre-
564 exercise (P \leq 0.04). ^EDifferent from end-exercise (P \leq 0.04).

565

566 **Figure 3** Neck thermal comfort (A), whole body thermal comfort (B), neck thermal sensation (C),
567 whole body thermal sensation (D), neck skin wettedness (E) and whole body skin wettedness (F) during
568 exercise and recovery (n=16, mean \pm SD). ^PDifferent from pre-exercise (P \leq 0.03). ^EDifferent from end-
569 exercise (P \leq 0.02).

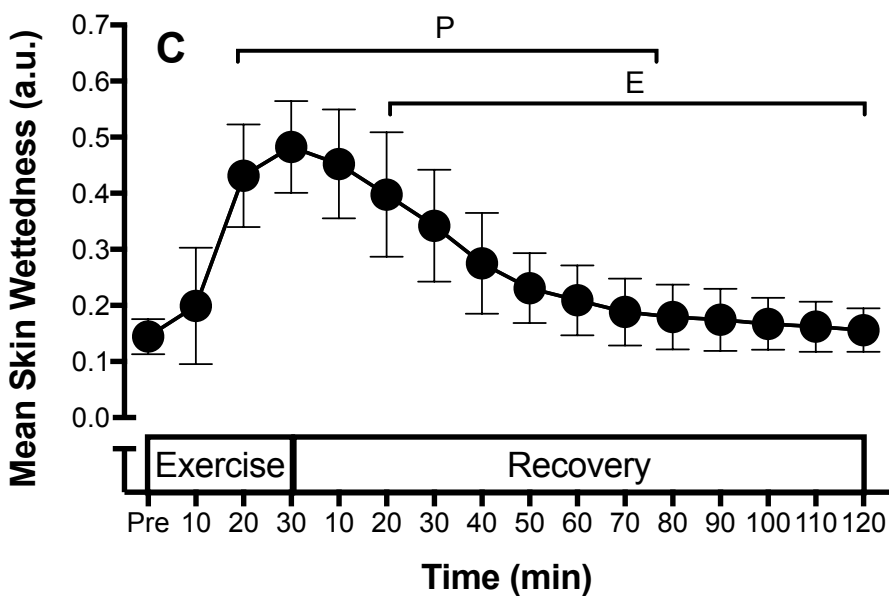
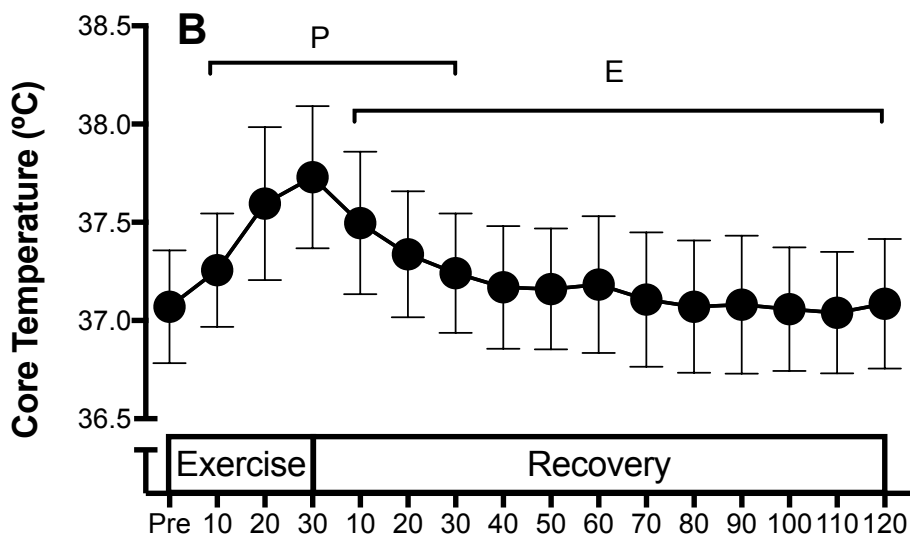
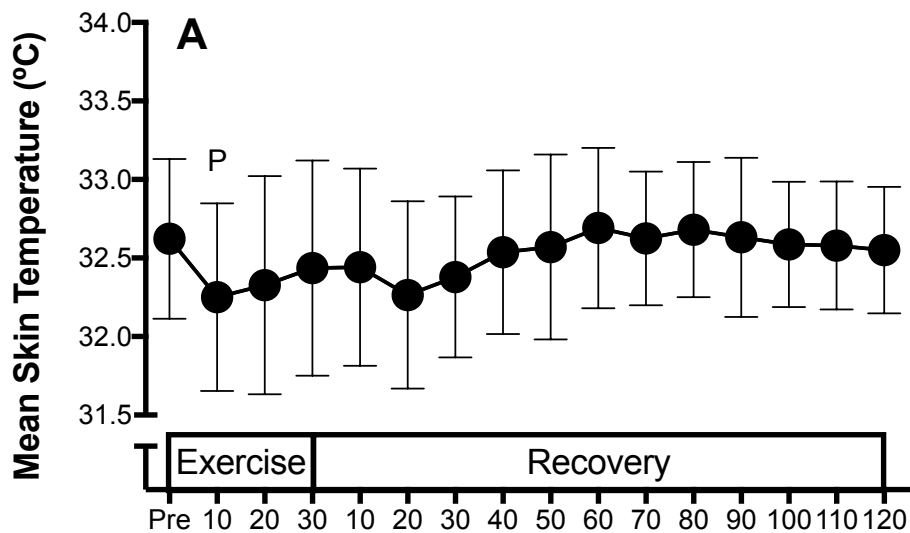
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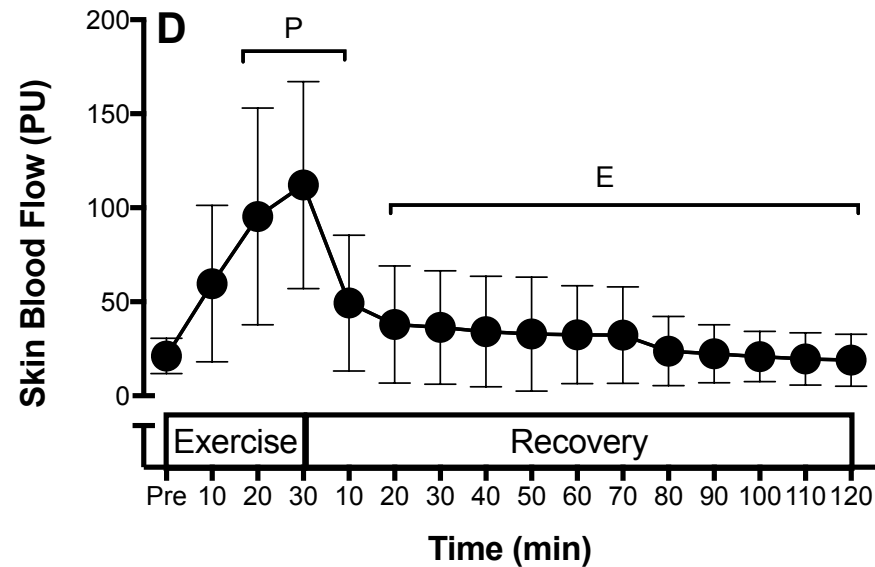
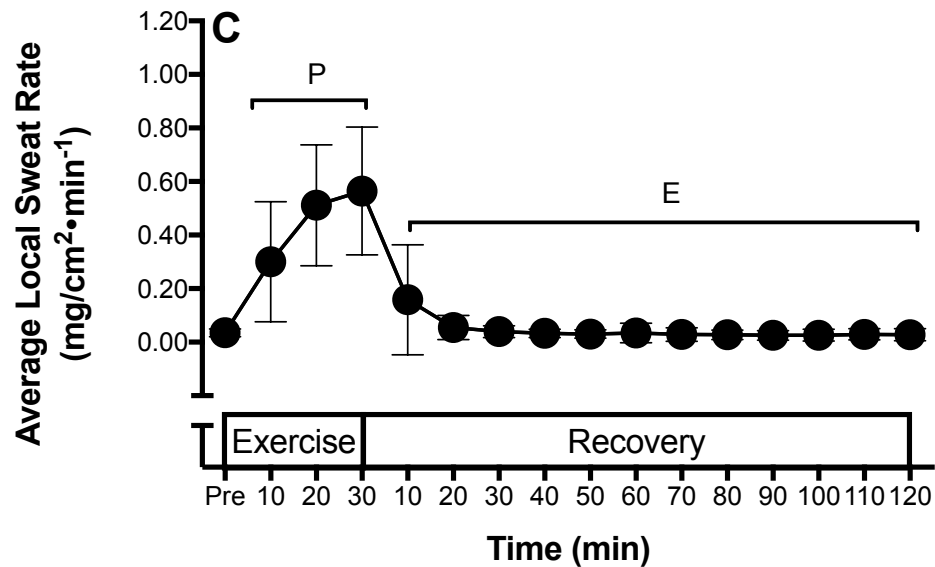
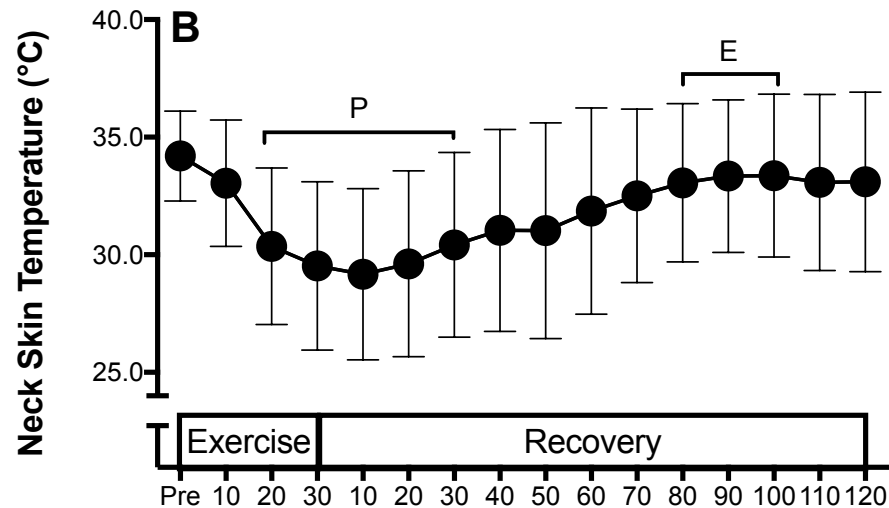
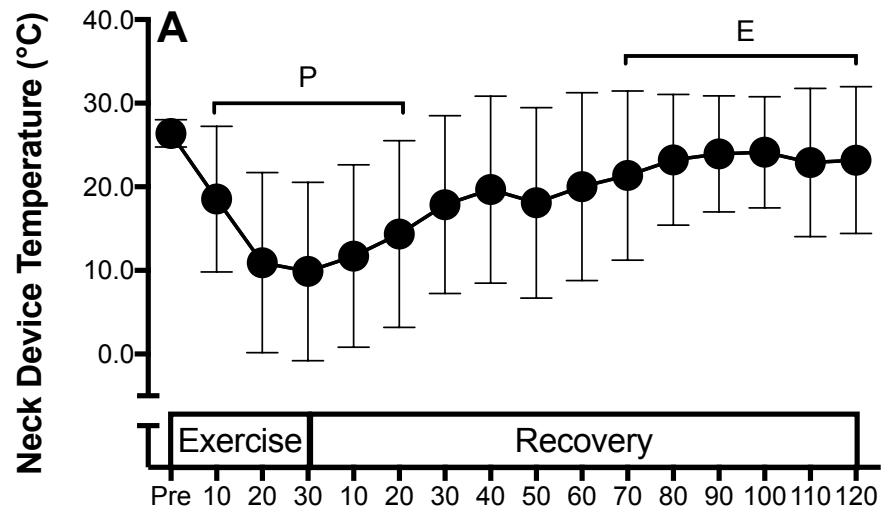
571 **Figure 4** Relative contributions of mean skin wettedness, core temperature and mean skin temperature
572 (n=14, mean \pm SD) to neck device temperature throughout the protocol. *Greater than mean skin

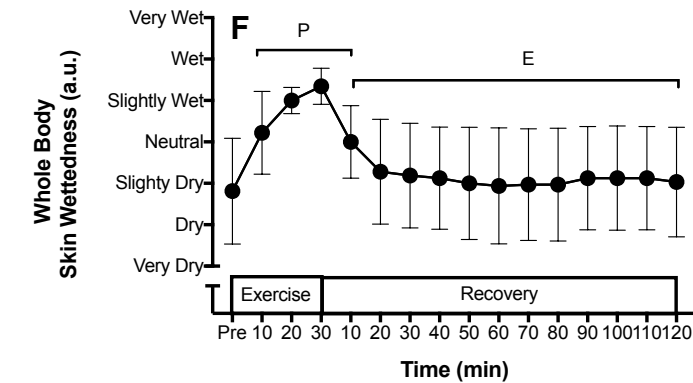
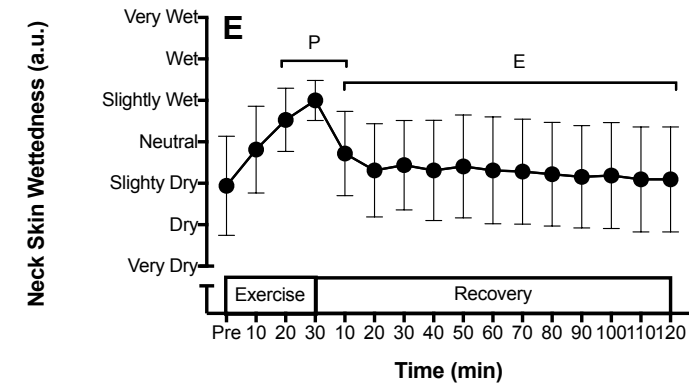
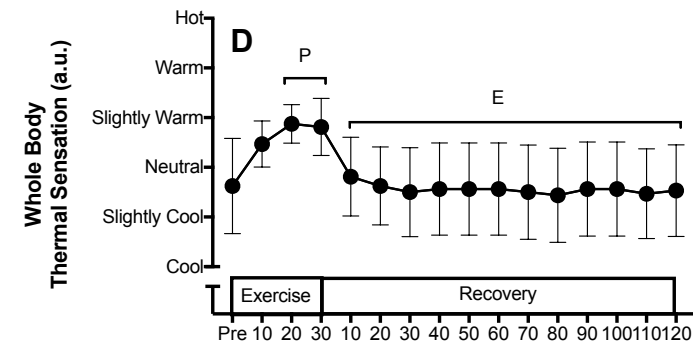
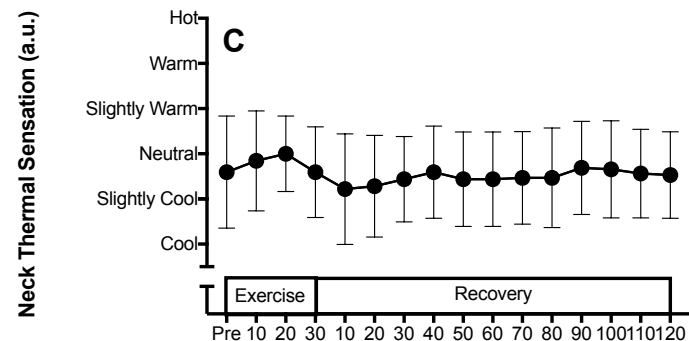
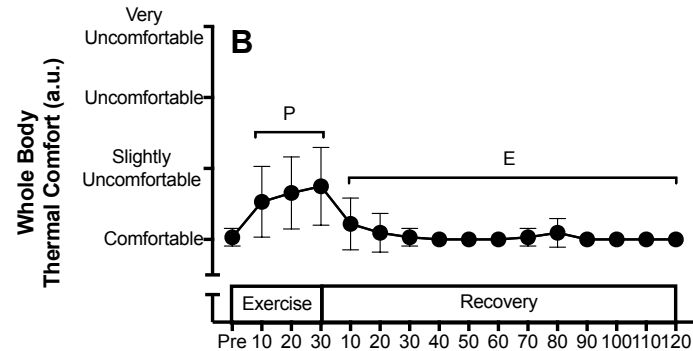
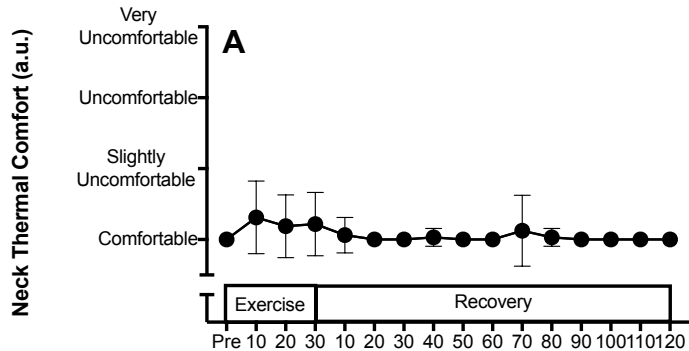
573 temperature (P=0.04).

Table 1. Subject Characteristics (mean \pm SD).

Number of subjects	16 (8 females)
Age (y)	23 \pm 3
Height (cm)	169 \pm 7
Weight (kg)	72 \pm 13
Body surface area (m ²)	1.82 \pm 0.20
Body fat (%)	15.5 \pm 6.8
VO ₂ peak (ml/kg/min)	41.8 \pm 7.0
Montreal Cognitive Assessment Score	29 \pm 1 ^a
^a all subjects were in the normal range (≥ 25) for age group (40).	







Relative Contribution to
Neck Device Temperature (%)

125
100
75
50
25
0

*



Skin Wettedness



Core Temperature



Skin Temperature

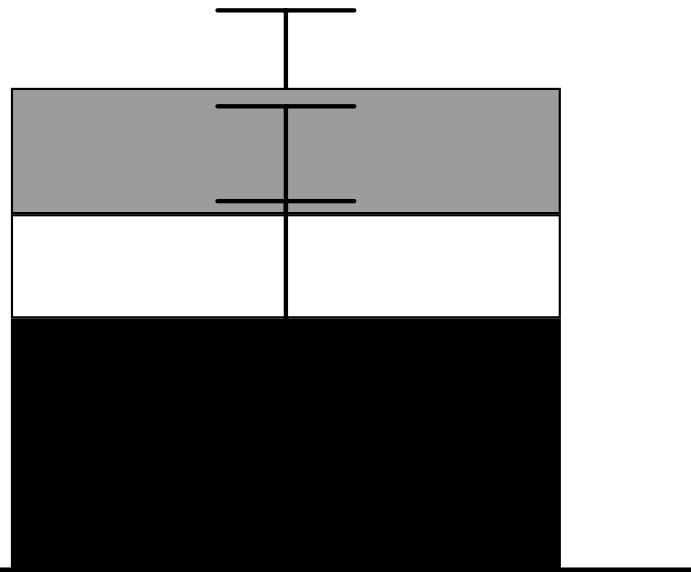


Table 2. Individual standardized beta coefficients (absolute values) for mean skin wettedness, core and mean skin temperatures to thermal behavior throughout the protocol (n=14)

Subject	Mean Skin Wettedness	Core Temperature	Mean Skin Temperature	R ²	P-value
1	0.444	0.109	0.451	0.741	<0.01
2	0.702	0.039	0.249	0.370	<0.01
3	0.269	0.196	0.323	0.570	<0.01
4	1.029	0.177	0.327	0.774	<0.01
5	1.001	0.135	0.018	0.783	<0.01
6	0.464	0.839	0.846	0.519	<0.01
7	0.176	0.333	0.487	0.355	<0.01
8	0.164	0.777	0.035	0.834	<0.01
9	0.999	0.481	0.654	0.529	<0.01
10	0.724	0.010	0.394	0.345	<0.01
11	0.939	0.003	0.076	0.955	<0.01
12	1.058	0.061	0.697	0.818	<0.01
13	0.371	0.419	0.076	0.634	<0.01
14	1.076	0.183	0.325	0.675	<0.01
Mean ± SD	0.673±0.349*	0.269 ±0.271	0.354±0.257	0.636±0.194	<0.01 ± 0.00
Standardized beta coefficients (absolute values) are from multiple linear regression with mean skin wettedness, core temperature and mean skin temperature as independent variables and neck device temperature as the dependent variable. *Greater than mean skin (P=0.04) and core temperatures (P=0.04).					